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Out of Indochina: confirmed specimen record and first molecular identification of *Psammophis indochinensis* Smith, 1943 (Squamata, Psammophiidae) from Bali, Indonesia

Nia Kurniawan[1*], Luhur Septiadi[2], Muhammad Fathoni[1], Gigih Setia Wibawa[1], Panupong Thammachoti[2]

1 Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Brawijaya, Malang, East Java, Indonesia • NK: wawan@ub.ac.id https://orcid.org/0000-0001-7383-8742 • MF: mfathni@gmail.com https://orcid.org/0000-0001-6500-9995 • GSW: siboleng@gmail.com

2 Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand • LS: luhur.septiadi@gmail.com https://orcid.org/0000-0001-5195-5550 • PT: panupong.th@chula.ac.th https://orcid.org/0000-0003-3477-8964

* Corresponding author

Abstract

Psammophis indochinensis Smith, 1943 was reported in the eastern Java and Bali of Indonesia despite its primary geographic range being in the Indochina region. We confirm its presence in Bali based on a newly collected specimen and provide morphological and genetic data. The specimen was found in a lowland, urban areas near open grassland habitat, which confirms the distribution of *P. indochinensis* along the northern coast of Bali. We note some character aberrations in the supralabials compared to Thailand specimens, suggesting an extended character. The basal clade position of *P. indochinensis* raises the possibility of an intercontinental dispersal scenario of this African-origin snake.

Keywords

Disjunct distribution, herpetofauna, reptile, snake, underestimated region

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Introduction

Psammophis indochinensis Smith, 1943, Indo-Chinese Sand Snake (Bahasa Indonesia: Ular Pasir Asia), is the only psammophiid snake species occurring in the Indochina region. This species is distributed in Myanmar, Thailand, Lao People's Democratic Republic (Lao PDR), Vietnam, Cambodia, and Indonesia, where it occurs in lowland habitats (Hartmann et al. 2011). However, there are few known occurrences of this species in Indonesia, where has been reported from East Java (Mertens 1957) and Bali (Ineich and Dueve 1990), or are doubtful (Kusrini et al. 2021). Based solely on these accounts, several field guides (McKay 2006; de Lang 2017; Somaweera 2017; Rusli 2020), include East Java and Bali within the range of *P. indochinensis*. Although an extensive

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survey in 2013–2019 has been conducted in Java, the species was not encountered at that time, and the previously reported specimen in the Museum Zoologicum Bogoriense (MZB) (Kurniawan et al. 2021) was presumably lost. Nonetheless, a recent survey in Bali Barat National Park (TNBB) in 2015 rediscovered this species (Amarasinghe et al. 2021), but unfortunately, voucher specimens were not collected (Amarasinghe pers. comm. 16 February 2021). As most members of genus *Psammophis* are primarily distributed in Africa, this has raised questions on the biogeographic history and taxonomic status of *P. indochinensis* (Kelly et al. 2008; Hartmann et al. 2011).

Herein, we confirm the presence of *P. indochinensis* in Bali based on a newly collected specimen. We provide morphological and genetic data, as well as updated information on the geographic distribution of this species and its congeners. The collected specimen is the first of *P. indochinensis* from Indonesia after three decades and includes genetic data. We discuss the possibility of intercontinental dispersal of this African-origin snake.

Methods

The individual of *Psammophis indochinensis* was caught by hand and immediately transported to the laboratory for examination. We recorded information on habitat, elevation, and geographic coordinates using a Garmin GPS Map 64s receiver. No scientific permits were needed as the voucher specimen was found in an urban area and not listed in the national protected fauna and flora of Indonesia under regulation by the Ministry of Environment and Forestry (PERMEN LHK; Ministry of the Environment 2018). Photographs were taken of the specimen alive in the laboratory (ex-situ) using a Nikon D5200 camera. The snake was euthanized with a dose of 7.5% benzocaine, fixed over 24 h in 10% formalin, preserved in 70% ethanol, and accessioned in the Laboratory of Animal Diversity and Ecology Collection, Biology Department, Universitas Brawijaya, Indonesia (NK), under the catalog number NK 2007. A tissue sample was collected in 95% ethanol for molecular study.

For the morphological characters, we compared the newly collected specimen (NK 2007) to four specimens available in Thailand Natural History Museum, Pathum Thani, Thailand (THNHM) including THNHM 1777–1779 and 1781, which collected by locals on 15 September 1965. We mapped the overall geographic distribution of *Psammophis* species (Fig. 6A) extracted from the literature (Supplemental file, Table S1), which corresponds to each representative clade on phylogenetic trees (Fig. 5). The geographical distribution of *P. indochinensis* was presented along with museum number (only for the collected specimens) obtained from Hartmann et al. (2011), Amarasinghe et al. (2021), and coordinates of the newly collected specimen. We used QGIS v. 3.8.1 (QGIS Development Team, Zürich, Switzerland) to map the geographic distributions of *Psammophis* species.

Scale counts and nomenclature of external morphology follow Peters (1964); the first number of ventral scales (first plate bordered on both sides by the first row of dorsals) follows Dowling's method (1951), and the terminal scute (precloacal plate) is not included in the number of ventrals. The dorsal scale row counts are given at one head length behind the head, at mid-body (one-half of the total number of ventrals), and one head length before the vent. The counts for paired head characters are listed in Table 2 in left/right order. All body measurements are to the nearest 0.1 mm. Character abbreviations follow Grismer et al. (2014): ASR = dorsal scale rows at neck, MSR = dorsal scale rows at mid-body, PSR = dorsal scale rows before vent, VEN = number of ventral plates, SC = number of subcaudal scales, ANA = anal plate single or divided, L = number of loreal scales, SL = number of supralabials, SL/Eye = number of supralabials touching eye, Larg SL = largest supralabial, IL = number of infralabials, IL/1st child = number of infralabials touching anterior chin shield, PreOc = number of preoculars, PostOc = number of postoculars, SuprOc = number of supraoculars, ATem = number of anterior temporals, PTem = number of posterior temporals, SVL = snout–vent length (mm), TaL = tail length (mm), TL = total length (mm), HL = head length measured from the caudal border of exoccipitals to the tip of snout (mm), HW = head width measured at the maximum width of head (mm), Rel TL = tail length relative to total length (TaL/TL×100), and Rel HW = head width relative to head length (HW/HL×100).

Mitochondrial DNA of the cytochrome b (cytB) gene was extracted from the liver and muscle tissue sample of the specimen NK 2007 using QIAamp DNA Mini Kit (Qiagen) following the manufacturer's protocol. We amplified and sequenced the cytB using primers H16064 (forward: 5′–CTTTGGTTTACAAGAACAATGCTTTA–3′) and L14910 (reverse: 5′–GACCTGTGATMTGAAAACCAYCGTTGT–3′) (Burbrink et al. 2000). Our derived sequence was deposited in GenBank (MZ970474) and compared with congeners (including 27 *Psammophis* taxa) and 2 outgroup taxa, *Psammophylax rhombeatus* (Linneaus, 1758) and *Dipsina multimaculata* (Smith, 1847), obtained from GenBank (Table 1). Sequences were aligned using ClustalW in MEGA v. 7 with default parameters (Kumar et al. 2016) and manually adjusted, resulting in 1,100 base pairs (439 parsimony-informative, 49 singleton sites, 612 constant sites). Uncorrected *p*-distance was calculated in MEGA v. 7 (Kumar et al. 2016). Nucleotide substitution model was estimated using jModelTest2 (Darriba et al. 2012). The GTR+G was considered as the best-fit substitution model for maximum likelihood (ML) and Bayesian inference (BI) of the cytB alignment. Phylogenetic inferences based on the ML was estimated using IQ-Tree (Nguyen et al. 2015) with 1,000 ultrafast bootstrap replicates (Hoang et al. 2018), and BI was estimated by

Table 1. Samples used in the molecular analyses with GenBank accession numbers. An asterisk (*) indicates identification of the species was changed from that provided by GenBank.

Species	GenBank AN	Country	Locality	Reference
Psammophylax rhombeatus	DQ486342	South Africa	Grahamstown	Kelly et al. 2008
Dipsina multimaculata	DQ486357	South Africa	Namaqualand	Kelly et al. 2008
Psammophis crucifer	DQ486360	South Africa	Somerset East	Kelly et al. 2008
Psammophis crucifer	DQ486397	Zimbabwe	Nyanga	Kelly et al. 2008
Psammophis jallae	DQ486409	Botswana	Kazungula	Kelly et al. 2008
Psammophis trigrammus	DQ486458	Namibia	Sesfontein	Kelly et al. 2008
Psammophis trigrammus	DQ486469	Namibia	Brandberg	Kelly et al. 2008
Psammophis lineolatus	DQ486450	Turkmenistan	Nephtezavodsk	Kelly et al. 2008
Psammophis condanarus	AF471075	Myanmar	Ayeyarwady Division	Lawson et al. 2005
Psammophis indochinensis	MZ970474	Indonesia	Buleleng Regency, Bali Province	This study
Psammophis angolensis	DQ486416	Zambia	Kabwe	Kelly et al. 2008
Psammophis angolensis	DQ486439	Botswana	Kasane	Kelly et al. 2008
Psammophis aegyptius	MG002976	Egypt	—	Gonçalves et al. 2018
Psammophis aegyptius	MG002972	Egypt	—	Gonçalves et al. 2018
Psammophis schokari	DQ486365	Morocco	—	Kelly et al. 2008
Psammophis schokari	AY612034	Tunisia	Bou Hedma	Gonçalves et al. 2018
Psammophis namibensis	DQ486455	South Africa	Port Nolloth	Kelly et al. 2008
Psammophis leightonii	DQ486467	South Africa	Piketberg	Kelly et al. 2008
Psammophis notostictus	DQ486362	South Africa	Grahamstown	Kelly et al. 2008
Psammophis notostictus	DQ486463	South Africa	Port Nolloth	Kelly et al. 2008
Psammophis praeornatus	MH997959	Senegal	Fafakourou	Trape et al. 2019
Psammophis punctulatus trivirgatus	DQ486432	Tanzania	Arusha Region	Kelly et al. 2008
Psammophis elegans univittatus	MK005679	Chad	Bon Amdaoud	Trape et al. 2019
Psammophis elegans	MH997943	Ivory Coast	Drekro	Trape et al. 2019
Psammophis tanganicus	DQ486378	Tanzania	Dodoma Region	Kelly et al. 2008
Psammophis tanganicus	DQ486379	Tanzania	Dodoma Region	Kelly et al. 2008
Psammophis biseriatus	DQ486389	Tanzania	Arusha	Kelly et al. 2008
Psammophis biseriatus	DQ486448	Kenya	Watamu	Kelly et al. 2008
*Psammophis lineatus**	FJ404313	Cameroun	—	Vidal et al. 2008
Psammophis lineatus	MH997938	Chad	Baïbokoum	Trape et al. 2019
Psammophis leopardinus	DQ486456	Namibia	Opuwo	Kelly et al. 2008
Psammophis leopardinus	DQ486462	Namibia	Grootberg Pass	Kelly et al. 2008
Psammophis philipsii	MH997952	Togo	Djiguengué	Trape et al. 2019
Psammophis philipsii	MH997955	Guinea	Kindia	Trape et al. 2019
Psammophis brevirostris	DQ486402	South Africa	Hole in the Wall	Kelly et al. 2008
Psammophis brevirostris	DQ486395	Zimbabwe	Marondera	Kelly et al. 2008
Psammophis sibilans	MH997970	Ethiopia	Kutaworje	Trape et al. 2019
Psammophis sibilans	MH997934	Egypt	Faiyum	Trape et al. 2019
Psammophis mossambicus	MH997940	Chad	Baïbokoum	Trape et al. 2019
Psammophis mossambicus	DQ486400	South Africa	Sodwana Bay	Kelly et al. 2008
Psammophis rukwae	DQ486443	Kenya	Lake Baringo	Kelly et al. 2008
Psammophis rukwae	MH997939	Chad	Baïbokoum	Trape et al. 2019
Psammophis afroccidentalis	MH997961	Burkina Faso	Pâ	Trape et al. 2019
Psammophis afroccidentalis	MH997960	Senegal	Dar Salam	Trape et al. 2019
Psammophis orientalis	DQ486380	Tanzania	Handeni	Kelly et al. 2008
Psammophis orientalis	DQ486396	Mozambique	Gorongosa	Kelly et al. 2008
Psammophis subtaeniatus	DQ486408	Botswana	Kazungula	Kelly et al. 2008
Psammophis subtaeniatus	DQ486415	Zimbabwe	Kariba	Kelly et al. 2008
Psammophis sudanensis	MH997948	Chad	Baïbokoum	Trape et al. 2019
Psammophis sudanensis	MH997950	Chad	Baïbokoum	Trape et al. 2019

MrBayes v. 3.2.7a (Ronquist et al. 2012) with Monte Carlo Markov Chains (MCMC) for 1,000,000 generations. Both were analyzed through the CIPRES Science Gateway (Miller et al. 2012). We visualized the trees using FigTree v. 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/), where colors for each clade (Fig. 5) correspond to overall geographic distribution of *Psammophis* species (Fig. 6A).

Results

Psammophis indochinensis Smith, 1943

Figures 1, 2, 3

New record. INDONESIA – **Bali Province** • Buleleng Regency, Gerokgak District; 08°09′29.40″S, 114° 42′56.80″E; 9 m alt.; 15.VI.2020; Gigih S. Wibawa leg.;

Figure 1. *Psammophis indochinensis* (NK 2007) from Gerokgak District, Buleleng Regency, Bali Province, Indonesia. **A.** In life (ex-situ). **B.** Entire dorsum. **C.** Entire ventrum. Photographs by M. Fathoni.

lowland and urban area near grassland habitat; 1 ♀, NK 2007.

The specimen was collected in broad daylight (10:00 h), moving fast around G.S. Wibawa's yard. This snake had possibly come from a nearby open grassland habitat (Fig. 4).

Identification. *Psammophis indochinensis* is the only species of its genus that occurs in Indochina. Its nearest congeners which are distributed mainly on the Indian subcontinent (i.e., *P. condanarus* (Merrem, 1820); *P. longifrons* Boulenger, 1890; *P. schokari* (Forskål, 1775); and *P. leithii* Günther, 1869) (Whitaker and Captain 2004; Hartmann et al. 2011; Vyas and Patel 2013). We identified the species using the key provided by Haidar et al. (2020): (1) smooth dorsals; (2) four chestnut-brown stripes, dorsally; and (3) two thin ventrolateral lines. *Psammophis indochinensis* is most similar to *P. condanarus* (characters in parentheses) but differs by the following diagnostic traits (Hughes 1999): (1) ventral scales fewer, numbering 156–173 (165–179); (2) subcaudal scales fewer, numbering 66–85 (75–93); (3) dorsal stripes four and lighter (dorsal stripes five and darker).

We compare our specimen with the scale ranges reported by Somaweera 2017 (characters in parentheses) as follows: 17:17:13 rows of smooth and shiny dorsals (17 or 19 at midbody); 163 ventrals (150–173); divided anal shield; and 27 paired subcaudals along

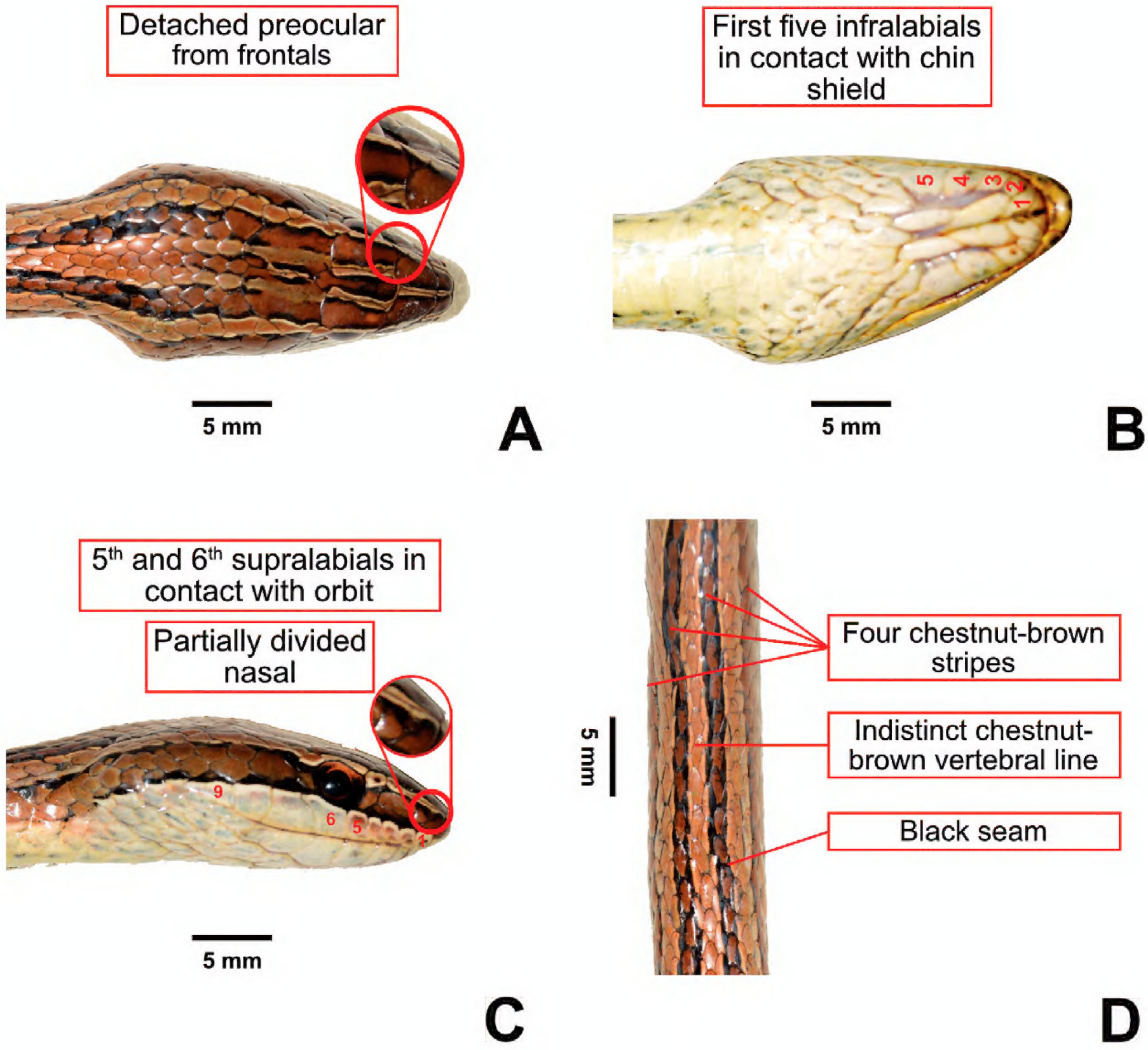

Figure 2. *Psammophis indochinensis* (NK 2007) from Gerokgak District, Buleleng Regency, Bali Province, Indonesia. **A.** Dorsal head. **B.** Ventral head. **C.** Right lateral head. **D.** Pattern of dorsum at midbody. Photographs by M. Fathoni.

an incomplete tail (75–85 in complete tails). The SVL of our specimen is 540 mm, HL is 19 mm, HW is 13 mm, and TaL is 57 mm but the tail is incomplete. Dorsal head surface shiny; rostral wider than high, hardly visible from above; internasals slightly longer than wide; prefrontals longer than wide; frontal narrowing posteriorly, elongate; supraoculars wider than frontal; parietals slightly shorter than frontal; two pair of chin shields, anterior larger than posterior; nasals partly divided, two times longer than high; two preoculars, upper part reaching top of head, not touching frontal; suboculars absent; two small postoculars; nine supralabials, fifth and sixth contacting orbit, seventh largest; 10 infralabials, first five in contact with chin shields; one temporal in 1st row followed by three temporals in 2nd row. In life, body pale olive, with four chestnut-brown stripes from snout to body, bordered by a narrow black margin, most prominent on midbody and anterior; head with an additional median stripe; chin and throat white and mottled with black; venter uniformly whitish yellow with two parallel thin longitudinal black ventrolateral lines from neck to tail (Figs. 1, 2, Table 2). Color after preservation dull and paler (Fig. 3). NK 2007 differs from THNHM 1777–1779 and 1781 (characters in parentheses) by having 5th and 6th supralabials contacting orbit (4th and 5th, collectively); higher Rel HW: 0.68 (0.50-0.61, collectively).

Phylogeny. Based on BI and ML phylogenetic analyses (Fig. 5), *P. indochinensis* is a sister taxon to the *P. condanarus* from Myanmar (clade 2). These closely related species differ from one another by an uncorrected *p*-distance of 0.0419 (4% in percentage; Supplemental file, Table S2). *Psammophis crucifer* (Daudin, 1803) from southern Africa (clade 1) and three Eurasian species—*P. lineolatus* (Brandt, 1838) from Turkmenistan, *P. condanarus* from Myanmar, and *P. indochinensis* from Indonesia—(clade 2) are the earliest-diverging lineages of the genus.

Figure 3. *Psammophis indochinensis* (NK 2007) from Gerokgak District, Buleleng Regency, Bali Province, Indonesia, after preservation. **A.** Entire dorsum. **B.** Entire ventrum. **C.** Left lateral head. **D.** Right lateral head. **E.** Dorsal head. **F.** Ventral head. Photographs by M. Fathoni.

Discussion

Morphological characters of *Psammophis indochinensis* have been reported from specimens from the Indochina region. In our Bali specimen (NK 2007), we noted aberrations in some characters (see above and Table 1). Haidar et al (2020) noted that the supralabials touch the eyes in both *P. condanarus* and *P. indochinensis*, which differs from *P. schokari* (4th and 5th vs. 5th and 6th), and NK 2007 had the 5th and 6th supralabials touching eye (Fig. 2C). Cox et al. (2012), Das (2012), and de Lang (2017) recognized *P. indochinensis* by having fewer supralabials (SL: 8), which differs from NK 2007 and THNHM 1777 which have nine supralabials (Fig. 2C). Thereby, characters on supralabials touching eye and total number of supralabials should be extended for *P. indochinensis*. Although the specimen from East Java (MZB 65 1) was lost (Kurniawan et al. 2021), the brief description of this specimen by Mertens (1957) showed that it is similar to Thailand specimens in having the 4th and 5th supralabials touching the eye. Additional comparisons of specimens, such as MNHN 1989-49 reported from Bali (Ineich and Dueve 1990), may reveal if this character state is unique to the Bali population.

Sex determination on our specimen was only possible by dissection, as sexual dimorphism (e.g., longer tail, longer SVL) was not observed in *P. condanarus* (Cottone et al. 2009) and most other species of *Psammophis* (de Haan 1999). Besides, sex determination using tail length character in *P. indochinensis* is impractical since most of our observed specimens had lost their tail. This is possibly due to caudal autotomy, which is an antipredator mechanism that is also possessed by other *Psammophis*

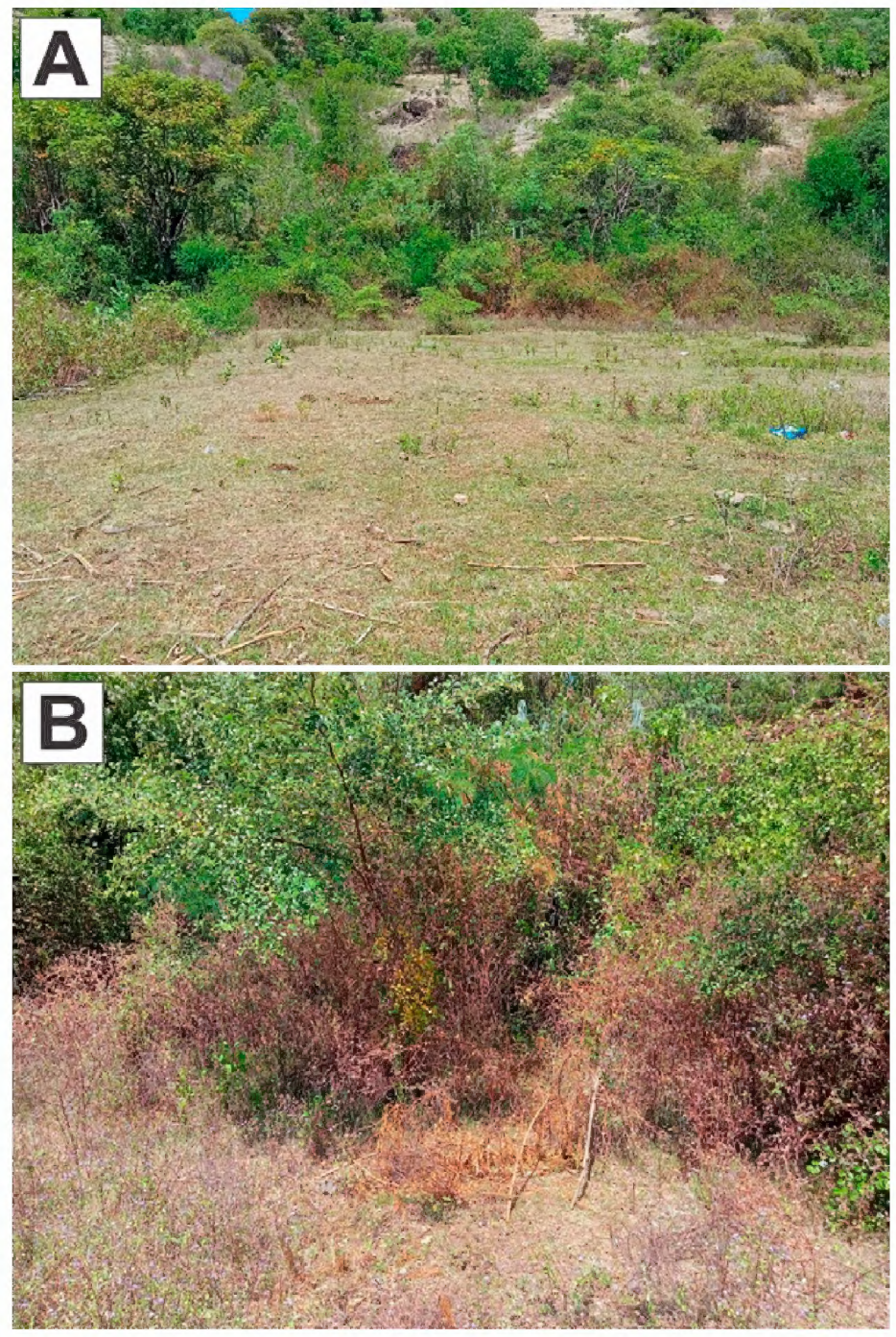

Figure 4. Landscape view where *Psammophis indochinensis* (NK 2007) was found in Gerokgak District, Buleleng Regency, Bali Province, Indonesia. **A.** Open grassland. **B.** Nearby dry grasslands habitat. Photographs by G. S. Wibawa.

species (Broadley 1987).

Our specimen was found in lowland and urban areas near open grassland habitats comprise of scattered vegetations (Fig. 4). *Psammophis indochinensis* has been previously reported in Borassus palm savannah near the sea (Ineich and Dueve 1990), in a wide range of habitats including grassland, open forest, agricultural areas, scrubland, and savannah (Das 2012; Rusli 2020), and in lowland deciduous monsoon forest and moist forest (Amarasinghe et al. 2021). The elevational range has been reported between 100 and 2000 m (McKay 2006; Das 2012), between 983 and 2000 m (Cox et al. 2012); and at sea level (new data herein). Considering those similar habitats and elevations are present on adjacent islands (e.g., Lesser Sunda), with more sampling it is likely that *P. indochinensis* may also be found to occur on nearby islands. Our new record eliminates the doubt by Kusrini et al. (2021) that *P. indochinensis* occurs in Indonesia.

We confirm the exact location of the species in Buleleng Regency (this study; NK 2007), as it was previously reported near Mount Merbuk in Bali of Indonesia (Ineich and Dueve 1990; MNHN 1989-49). This species also occurs at Bali Barat National Park (TNBB) (Amarasinghe et al. 2021), 26 km west from Buleleng Regency. In Java, it was recorded in Gresik of East Java (Mertens

Table 2. Scalation and measurement of *P. indochinensis* from Indonesia (NK 2007) and Thailand (THNHM 1777–79 and 1781). Abbreviations are listed in the Methods. An en dash (–) indicates that the tail was incomplete.

Specimen ID	THNHM 1777	THNHM 1778	THNHM 1779	THNHM 1781	NK 2007
Locality	Thailand				Indonesia
	Pathum Thani	Pathum Thani	Pathum Thani	Pathum Thani	Bali
SEX	♀	♀	♀	♀	♀
ASR	17	17	19	19	17
MSR	17	16	17	17	17
PSR	12	13	13	13	13
VEN	161	164	171	167	163
SC	71	28 (–)	83	76	27 (–)
ANA	Single	Single	Single	Single	Single
L	1/1	1/1	1/1	1/1	1/1
SL	9/9	8/8	8/8	8/8	9/9
SL/Eye	4.5/4.5	4.5/4.5	4.5/4.5	4.5/4.5	5.6/5.6
Larg SL	7/7	6/6	7/7	6/6	7/7
IL	10/10	10/10	10/10	10/10	10/10
IL/1st child	4/4	4/4	4/4	4/4	4/4
PreOc	2/2	1/1	1/1	1/1	2/2
PstOc	2/2	2/2	2/2	2/2	2/2
SuprOc	1/1	1/1	1/1	1/1	1/1
ATem	2/2	1/1	1/1	1/1	1/1
PTem	3/3	3/3	3/3	3/3	3/3
SVL (mm)	649.0	349.0	452.0	374.0	540.0
TaL (mm)	214.0	113.0 (–)	153.0	112.0	57.0 (–)
TL (mm)	863.0	462.0 (–)	605.0	486.0	597.0 (–)
HL (mm)	20.1	13.1	13.5	13.3	19.1
HW (mm)	10.1	8.1	8.3	8.0	13.0
Rel TL	0.24	0.24 (–)	0.25	0.23	0.9 (–)
Rel HW	0.50	0.61	0.61	0.60	0.68

1957; MZB 65 1), 252 km northwest from Buleleng Regency. In Indochina region, it was recorded in Phetchaburi Province of Thailand (Pauwels et al. 2003), more than 2700 km north of Bali and East Java, which means that this species has a highly disjunct distribution. This distribution pattern is similar to the *Daboia siamensis* (Smith, 1917), which is primarily distributed in Indochina region but has been recorded in East Java and on Lesser Sunda and inhabiting seasonally dry climates (de Lang 2017; Kurniawan et al. 2021). One may argue that the occurrence of *P. indochinensis* in Indonesia was accidentally introduced by trade (Liong, 1958) or transported with wood, as reported by Mertens (1957) for *P. sibilans* (Linnaeus, 1758). Previous phylogenetic studies (Kelly et al. 2008) and our phylogenetic trees (Fig. 5) showed that not only *P. indochinensis*, but also *P. condanarus* and *P. lineolatus* (Eurasian taxa) are the earliest-diverging lineages of *Psammophis*. This raises interesting questions on its biogeographic history and leads us to hypothesize the possibility of the intercontinental dispersal scenario of this African-origin snake.

Disjunct distribution among closely related taxa across continent is not uncommon and has been reported in lizards (Brandley et al. 2011), rat snakes (Burbrink and Lawson 2007), iguanas (Keogh et al. 2008), crocodiles (Oaks 2011), vipers (Wüster et al. 2008), and hinged-teeth snakes (Chen et al. 2013). The family Psammophiidae first emerged around 30 Mya (Zaher et al. 2019) in Africa. Our phylogenetic analysis indicates that the most recent common ancestor of the earliest diverging and extant taxa (i.e., *P. indochinensis*, *P. condanarus*, and *P. lineolatus*) may be distributed via the Gomphotherium landbridge which connected the Eurasian and Afro-Arabian plates around 15 Mya (Rögl 1999) after the Arabian plate was separated from the African plate by the formation of the Red Sea around 25 Mya (Bosworth et al. 2005). At that time, the most recent common ancestor of the earliest diverging and extant taxa may have successfully colonized Eurasia in suitable habitats of dry deciduous forests, scrub, and savannah along the coast of central-southeast Asia (Morley 2018).

The next major process was the extirpation of these most recent common ancestors in the Arabian and African plates. If these recent common ancestors successfully colonized Eurasia continent, this indicates that they were once present in Arabian and African plates. Due to the progressive aridification, geological instability, and climatic changes in Arabia and Africa plates during the Miocene and Plio-Pleistocene (Tejero-Cicuéndez et al. 2020), *Psammophis* may have radiated into many clades in the southern, western, and northern coasts of Africa as well as the central part of the continent, similar to *Acanthodactylus* (Tamar et al. 2016). Presumably the earliest diverging *Psammophis* species in Africa and Arabia went extinct due to the aridification, although this is weakly supported due to the lack of extant species. The low species diversity in the Eurasian lineage (only three extant species), may be due to increased extinction rates

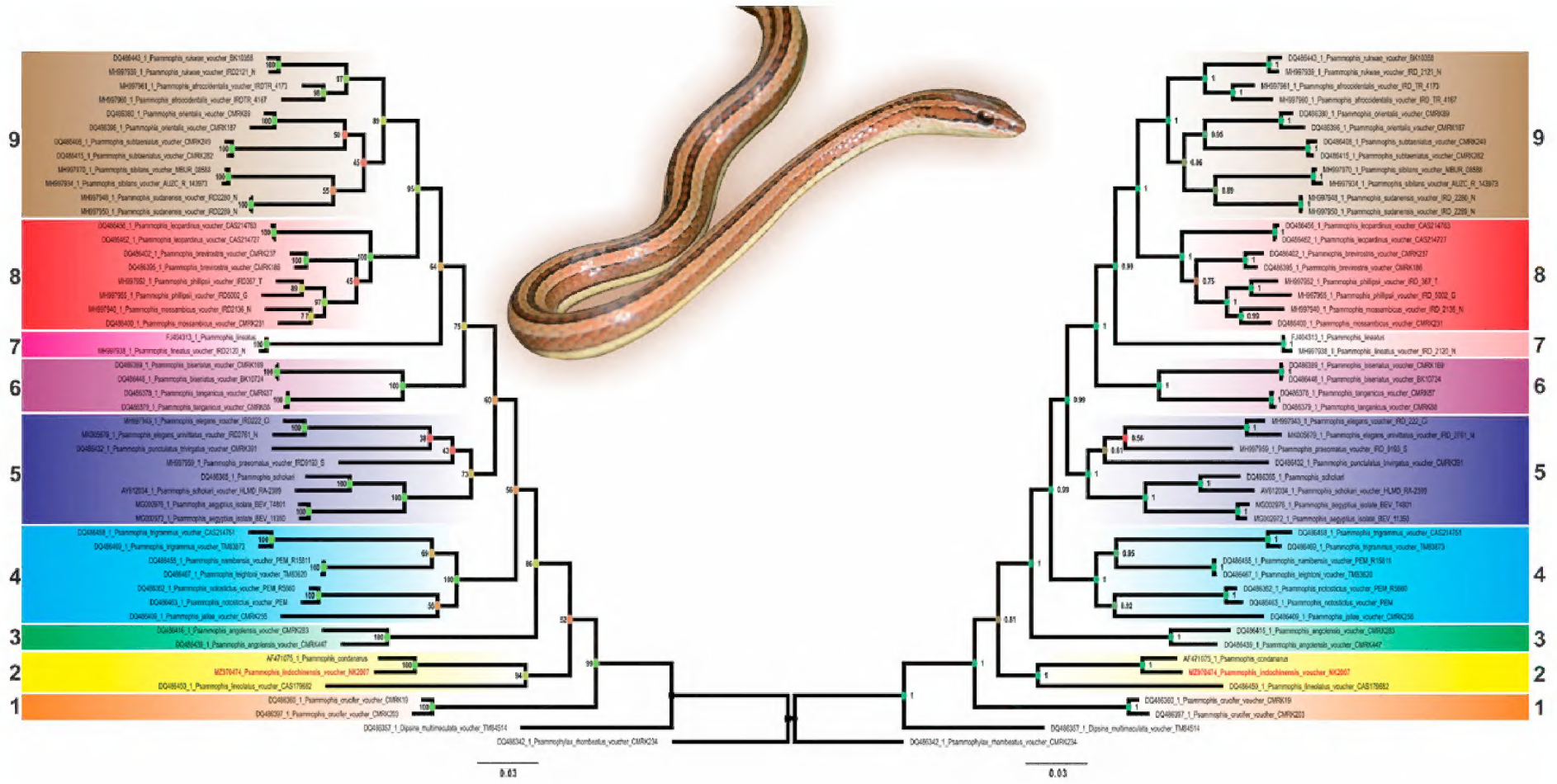

Figure 5. Maximum likelihood (ML; left) and Bayesian inference (BI; right) trees of cytB alignment showing the basal clade position of *Psammophis indochinensis* (NK 2007) from Gerokgak District, Buleleng Regency, Bali Province, Indonesia. The bootstrap supports for ML and Bayesian posterior probability for BI are indicated by numbers and colors (ML: 0–100, BI: 0–1; green: strongly supported, red: weakly supported). Sequence generated in this study is shown in red type.

as a result of environmental pressures and/or reduced speciation rate (Burbrink and Pyron 2010).

Similar to the above scenario, the occurrence of *P. indochinensis* in Indonesia could be explained by inquiring to last glacial period (LGP), when the "Savanah corridor" existed through the Sundaland continent (Bird et al. 2005). This corridor—formerly proposed by Heaney (1991)—encompassed some parts of the present-day Gulf of Thailand, eastern coast of peninsular Malaysia, Java Sea, eastern Java, and Bali. This corridor may have provided a distribution route for *P. indochinensis* to Bali, leading to the possibility of intercontinental dispersal. This corridor submerged due to a sea-level rising after the LGP, leaving only several savannahs in eastern Java and Bali. By inference, this hypothesis supports the previously reported occurrences of *P. indochinensis* in East Java and Bali (Mertens 1957; Ineich and Dueve 1990), which would mean that this species is native there. However, this explanation can only be justified by further analysis of a divergence time estimation.

Overall, our new record provides additional data on the distribution and morphological variation required for resolving the biogeographical history of *P. indochinensis*. Continuous and intensive survey efforts will surely yield more knowledge on the extent of distribution of herpetofauna species in these regions.

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Authors' Contributions

Conceptualization: NK. Data curation: MF. Investigation: NK, GSW, PT. Resources: GSW, PT. Visualization: MF. Writing – original draft: NK. Writing – review and editing: LS.

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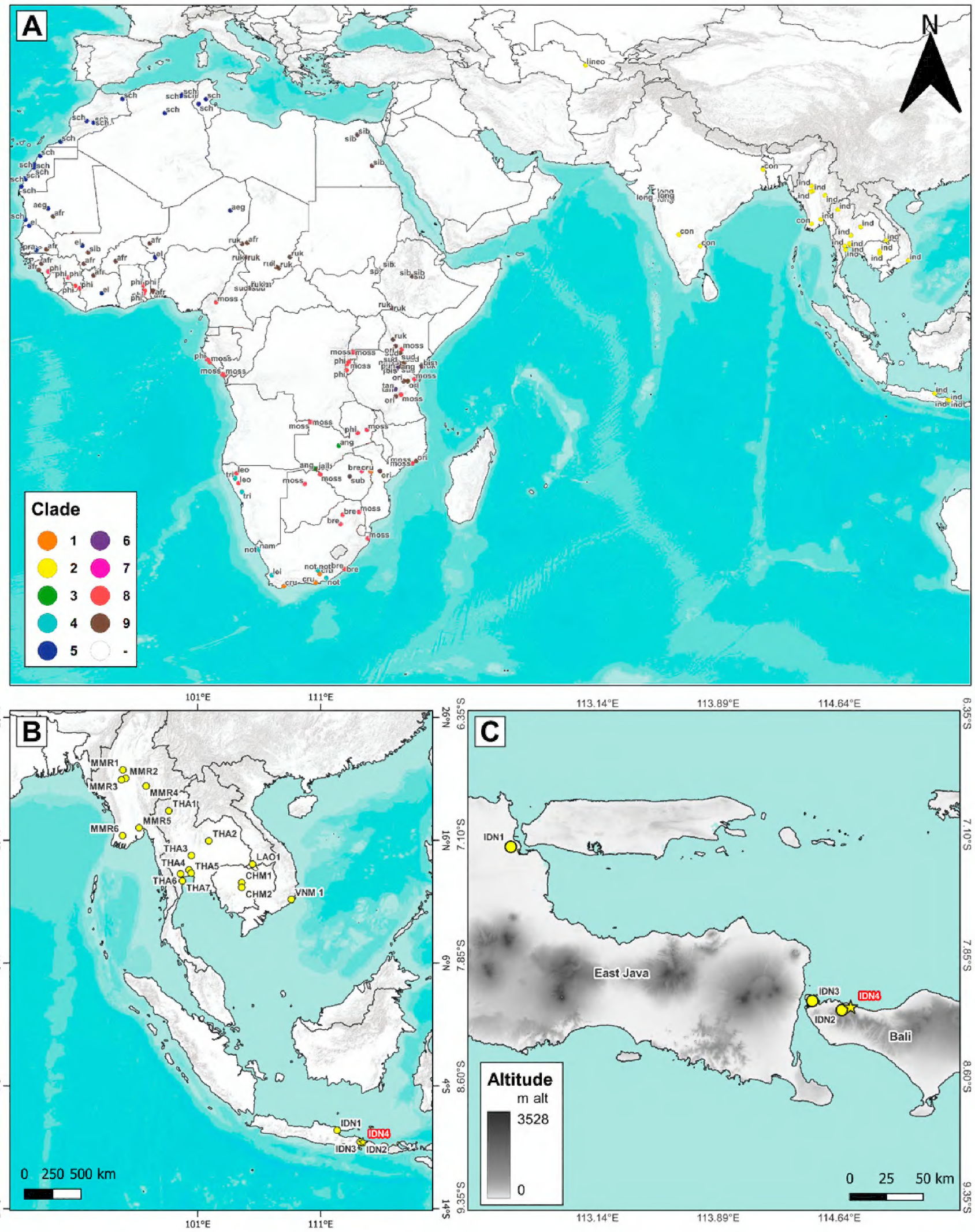

Figure 6. Overall geographic distribution of several *Psammophis* members in Africa and Eurasia. **A.** Distribution of *Psammophis* in Africa and Eurasia. Abbreviations for Fig. 6A are as follows, Clade 1: (cru) *P. crucifer*; Clade 2: (con) *P. condanarus*; (ind) *P. indochinensis*; (lineo) *P. lineolatus*; Clade 3: (ang) *P. angolensis*; Clade 4: (jall) *P. jallae;* (lei) *P. leightoni*; (nam) *P. namibensis*; (not) *P. notostictus*; (tri) *P. trigrammus*; Clade 5: (aeg) *P. aegyptius*; (el) *P. elegans*; (pra) *P. praeornatus*; (pun) *P. punctulatus trivirgatus*; (sch) *P. schokari*; Clade 6: (bis) *P. biseriatus*; (tan) *P. tanganicus*; Clade 7: (linea) *P. lineatus*; Clade 8: (bre) *P. brevirostris*; (leo) *P. leopardinus*; (moss) *P. mossambicus*; (phi) *P. phillipsii*; Clade 9: (afr) *P. afroccidentalis*; (ori) *P. orientalis*; (ruk) *P. rukwae*; (sib) *P. sibilans*; (sub) *P. subtaeniatus*; (sud) *P. sudanensis*; Clade – (not included in trees): (long) *P. longifrons*; (sp.); *Psammophis* sp. (see Supplemental material, Table S1 for details); where the color of dots corresponds to their respective clade (Fig. 5). **B.** Distribution of *P. indochinensis* in Indochina region and Indonesia. **C.** Distribution of *P. indochinensis* in Bali and Java. Abbreviations for Figs. 6B–C are as follows, MYANMAR: (MMR1) Sagaing Division (Wogan et al. 2008); (MMR2) Mandalay Division (Wogan et al. 2008); (MMR3) Magwe Division (Wogan et al. 2008); (MMR4) Shan State (Boulenger 1896); (MMR5) Bago Division (Boulenger 1890); THAILAND: (THA1) Chiang Mai Province (Taylor 1965); (THA2) Chaiyaphum Province (Das 2010); (THA3) Lopburi Province (Smith 1943); (THA4) Pathum Thani (this study; THNHM 1777–79, 1781); (THA5) Bangkok (Smith 1943; ZFMK 16 658); (THA6) Ratchaburi Province (Chan-Ard et al. 1999); (THA7) Phetchaburi Province (Pauwels et al. 2003); LAO PDR: (LAO1) Champasak Province (Stuart 1998; Teynié et al. 2004); CAMBODIA: (CHM1) Siem Reap Province (Hartmann et al. 2011); (CHM2) Kampong Thom Province (Hartmann et al. 2011); VIETNAM: (VNM1) Ninh Thuan Province (Smith 1943, Nguyen et al. 2009; ZFMK 88 831); INDONESIA: (IDN1) Gresik, East Java Province (Mertens 1957; MZB 65 1); (IDN2) Mount Merbuk, Bali Province (Ineich and Dueve 1990; MNHN 1989-49); (IDN3) Bali Barat National Park, Bali Province (Amarasinghe et al. 2021); (IDN4) Buleleng Regency, Bali Province (this study; NK 2007).

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Supplemental Materials

Table S1. Species abbreviations, locality, latitude and longitude (in decimal minutes; datum WGS 84), and specimen ID of taxa used to map the overall geographic distribution of Psammophis species in Africa and Eurasia (Fig. 6) corresponds to their respective clade (Fig. 5).

Table S2. Uncorrected *p*-distance between cytB sequences of *Psammophis* species included in phylogenetic analysis.